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Behavioural phylogeny of Bovidae

Pierre Deleporte^{1*} & Henri Cap²

¹Université de Rennes 1, CNRS, UMR6552 EthoS, Station Biologique, 35380 Paimpont, France.

²Muséum d'Histoire Naturelle de Toulouse, 31000 Toulouse, France.

*Author for correspondence and reprint requests; E-mail: pierre.deleporte@univ-rennes1.fr

Abstract

In this article, we examine the possible contribution of behavioural studies to the determination of phylogenetic relationships within the Bovidae. First, we revisit the general arguments concerning the use of behavioural traits as phylogenetic characters; then we present our first attempt at reconstructing the phylogeny of Bovidae based on behavioural data taken from the literature. Despite the limited number of characters used, several clades of low hierarchical levels are supported by this phylogenetic analysis, in much the same manner as by morphological and molecular ones. Several characters linked to male sexual behaviour appear to be among the more informative ones.

Key words: Phylogeny, behaviour, Bovidae, methods.

1. Introduction

Methods for phylogenetic inference are undergoing tremendous changes with the advent of molecular approaches. This does not mean that the more traditional morphological and behavioural approaches should now be completely neglected. Both have proved successful in unraveling some well supported phylogenetic relationships. In the ongoing debates about the phylogeny of ruminants, we believe that behavioural characters could play a role, provided that more extensive and detailed work is developed in this direction. Given the lasting controversies about the merits of different kinds of characters for phylogenetic inference, we first review the classic arguments for and against the use of behavioural characters for phylogenetic inference. We then propose a preliminary phylogenetic analysis of Bovidae based on behavioural characters collected from the literature.

2. Behavioural phylogenetics: methodological considerations

The use of behavioural characters in phylogenetics is still a controversial topic. Mapping these characters on a phylogeny independently inferred from morphological or molecular characters to study the evolution of behaviour does not raise many objec-

tions; however, basing phylogenetic inference upon behavioural traits is not universally accepted. Early ethologists had no such reluctance. The founders of behavioural sciences were keen to demonstrate that behavioural characters, much like morphological ones, could provide relevant taxonomic evidence. Even if genuine and explicit phylogenetic methods were not immediately implemented, a taxonomic work like that of Lorenz (1941) on anatid birds, later developed by Johnsgard (1961) under the name of evolutionary relationships of Anatidae, produced *de facto* phylogenetic patterns based on behavioural characters, largely in accordance with morphology-based phylogenetic relationships (Irwin 1996). Later on, many ethologists focused mainly on epigenetic processes driving the emergence of the more plastic aspects of behaviour. More recently, there has been a resurgence of interest in comparative ethology due to theoretical developments in the study of behavioural evolution (like sociobiology) and methodological developments (phylogenetic systematics and computer-assisted inference methods). These advancements have allowed comparative ethology to take an explicit phylogenetic perspective. In this context, differing opinions have been expressed regarding the possible use of behavioural characters in phylogenetic inference. Atz (1970) stands among the radical opponents, negating the possibility of homologizing behavioural traits among different species, limiting the focus to only morphological and

physiological traits. However, Atz (1970) concedes that among the “most convincing examples of homologous behavior” are the “patterns of locomotor activities that are found in a single group of related species and in all the members of the group. Not to conclude that such behavior was also practiced by the common ancestor [...] would violate the principle of parsimony.” Hence, despite his reticence, Atz accepted to consider uniquely derived and unreversed characters as homologies, which finally appears as a conservative application of the ‘maximum parsimony’ principle regularly used in phylogenetics. On the other hand, Wenzel (1992) developed a detailed and balanced argument in favor of the use of behavioural characters for phylogenetic inference. He listed 23 authors who generated phylogenies from behavioural data. De Queiroz & Wimberger (1993) showed, from bibliographical analysis, that behavioural characters were no more homoplastic than morphological characters.

Without going through a detailed analysis, some arguments need to be made. The question of homology assessment for behavioural characters is rather straightforward. Basically, the classical homology criteria – *position*, *connection by intermediates*, and *special quality* – are applicable to behaviour, although in some specific ways (Wenzel 1992). Ever since early ethological approaches, *position* is deduced through the succession of behavioural items in behavioural sequences. Molecular phylogeneticists proceed in a similar way when using the position of base pairs in otherwise “aligned” homologous sequences of DNA. Behavioural sequences may be both much shorter and much more diverse in their components. Classical sequence analysis dealt with complex stereotyped behavioural patterns. More recently, analyses of behavioural sequences within social interactions of insects have used elementary successions of specific behavioural actions, with convincing phylogenetic results (successive event-pairing method, Legendre et al. 2008, 2014). *Connection by intermediates* is used for diagnosing variants of a behavioural pattern as likely homologous character states of a unique behavioural character progressively modified through a continuous evolution in closely related taxa. Secondary plotting on the phylogeny will tell the optimal evolutionary scenario for the character, but the necessary a priori homology assessment is done through direct comparison of behavioural variants. *Special quality* is generally considered as the more useful criterion, particularly for highly diverse kinds of behavioural traits, hence limiting the risks of misleading homoplasy. This criterion can be augmented with consideration of the function of behaviour, via the analysis of its context of expression, but function alone is hardly usable given the range of possible ways to fulfill a similar function.

A common objection against the use of behavioural characters in phylogenetic inference is the al-

leged high plasticity of behavioral traits. Of course relevant phylogenetic characters are supposed to be heritable, and not just culturally or environmentally acquired and modified. Hence plastic behaviors, or the plastic parts of otherwise stereotyped behavioural sequences, should be identified. This can be done through careful and extensive observations. Ideally, individuals and groups of individuals of the different species should be observed under varying developmental and environmental contexts, when some epigenetic plasticity is suspected. Serial comparative experiments using many individuals in controlled contexts are tractable in easily bred species (for example insects, Legendre et al. 2008, 2014). Of course this is more difficult for free ranging and rare or cryptic animals. Extensive observational studies of behavior under comparable conditions are very demanding, but this is a practical, not a theoretical limit.

Concern has been raised about using behavioural characters for phylogenetic inference and then describing the evolution of these characters based on the reconstructed phylogeny: this should allegedly be avoided to escape the flaw of circular reasoning; e.g. Brooks & McLennan (1991) raised this point as a “cardinal rule”. In fact, this would be true only if one would use just a single behavioural character for phylogeny inference, and then draw an optimal evolutionary scenario for the same character from the phylogenetic topology. When many phylogenetic characters are used and the optimal phylogenetic topology is identified through overall congruence among character distributions, no tautology or vicious circular reasoning is ever involved (Deleporte 1993; Grandcolas et al. 2001). Brooks & McLennan (2002) came to the same conclusion: “Use all available evidence to construct your phylogenetic hypothesis, but be sure that the phylogenetic tree being used to investigate the evolution of trait x depicts relationships that are maintained when trait x is excluded from the analysis”.

Phylogenetic inference is an exercise in the “plausible narrative” (Clauss & Rössner 2014) for which *all relevant evidence* must be used (in the broadest sense of *all relevant knowledge*; i.e. not just all the characters (or “all the data”) but also all we can know about them - Lecomte & Deleporte (2005). Traits of dubious homology should be avoided (e.g. Grandcolas et al. 2011), but all valid, informative characters should be used. There is no reason to discard any potentially informative evidence. Restricting evolutionary studies of behavioural characters to plotting them on an independent phylogeny hardly makes sense, because the criteria for inferring an optimal evolutionary scenario are the same as those for selecting phylogenetic characters in the first place: i.e. reliability of their primary homology. Whatever kind of characters is concerned; when a character is valid for evolutionary scenario optimization, it is also valid for taking part in the data matrix for phylogenetic inference (Grandcolas et al. 2001).

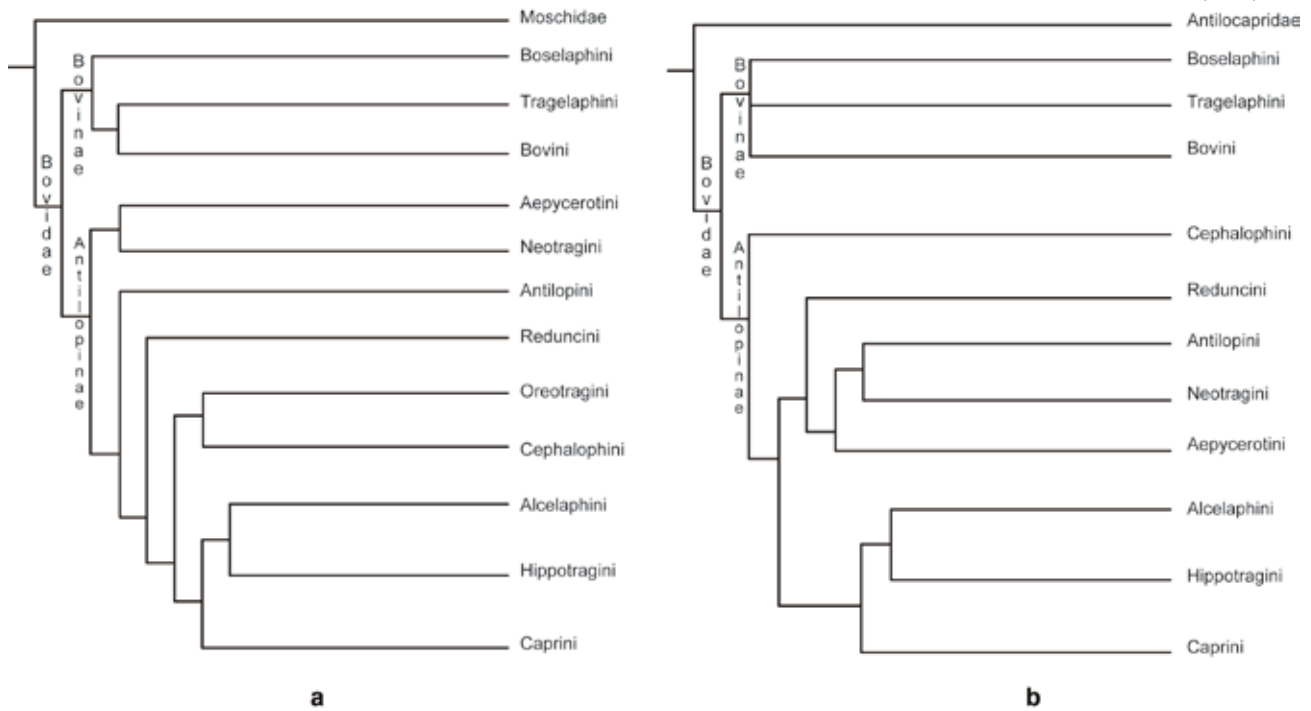


Figure 1: (a) Phylogenetic topology (ML) of Bovidae inferred from mtDNA (Hassanin et al. 2012). **(b)** Phylogenetic topology (MP) of Bovidae inferred from morphology and behaviour (Vrba & Schaller 2000).

A last important question is how to combine different kinds of characters for phylogenetic inference. Ideally, biologists should understand the principles of character evolution and use this background knowledge to devise models for the analysis of different kinds of characters. Molecular analyses regularly implement explicit models of character change, required in maximum likelihood approaches. In morphological and behavioural phylogenetics, we tend to use equal “weights”, “costs” or probabilities of change for all characters, largely because we do not know how to determine relative weights for the alternatives. It must be noted that “equal weights” for any character transformation in maximum parsimony phylogeny inference is not an absence of a model, but a particular evolutionary model (coined as NCM - for “No Common Mechanism” - by Tuffley & Steel 1997). Performing separate phylogenetic analyses for different kinds of characters does not really solve the problem, because the question will remain of how to balance the contribution of the different tentatively inferred phylogenies. By this somewhat pessimistic observation, we simply want to stress that, in the present state of biological knowledge, any phylogenetic inference should be taken very cautiously, given the risk of overestimating the resolution of the phylogenetic topology. Fortunately, we can be rather confident in the historical accuracy of the clades most strongly supported by different sources of evidence, assuming that these inferences would resist some range of approximation in character coding and evolutionary models.

In the following analysis, we will adhere to a classic, uniformly-weighted, parsimony approach, because appropriate weighting schemes for alternatives are not known.

3. Behavioural phylogeny of Bovidae

Bovidae is the most diversified family of the order Cetartiodactyla (species numbers vary from ≈ 142 to ≈ 300 depending on the species concept used). Recent molecular studies have reached a consensus with morphological approaches at higher phylogenetic levels (Hassanin et al. 2012), but several relationships remain unresolved when compared to the results of the combined morphological and behavioural phylogenetic analysis by Vrba & Schaller (2000). Both topologies are presented in Fig. 1. In this study, we will first describe the taxonomic distribution of diverse behavioural characters in ruminants, and then describe how comparative ethologists may derive patterns of behavioural evolution without a specific phylogenetic reference. Finally, we will use these characters for a tentative phylogenetic inference based solely on behavioural characters.

3.1 Data sources and methods

3.1.1 Taxa and character sampling

In this study, 42 bovid taxa were considered (Tab. 1). We analyzed the complete behavioural data set studied by Walther (1974), using his tables and additional data from the text of the same chapter. Walther classed the 39 behavioural characters in three categories: threat displays (postures, 12 characters), dominance postures expressed in hostile encounters (9 characters) and patterns of male courtship displays (18 characters). These characters are listed and defined in Tab. 2. In the corresponding data matrix for phylogenetic analysis (Tab. 3), the absence or pre-

Table 1: Taxa analyzed in this study (bibliographic source: Walther, 1974).

Taxon	Common name
Bovinae	
Bovini:	
<i>Bos taurus</i>	cow
<i>Bos gaurus</i>	gaur
<i>Bison bison</i>	American bison
Boselaphini:	
<i>Boselaphus tragocamelus</i>	nilgai
Tragelaphini:	
<i>Tragelaphus scriptus</i>	bushbuck
<i>Tragelaphus spekei</i>	sitatunga
<i>Tragelaphus angasi</i>	nyala
<i>Tragelaphus imberbis</i>	esser kudu
<i>Tragelaphus strepsiceros</i>	greater kudu
<i>Taurotragus oryx</i>	common eland
Antilopinae	
Cephalophini:	
<i>Cephalophus nigrifrons</i>	black fronted duiker
Antilopini:	
<i>Raphicerus campestris</i>	steenbok
<i>Madoqua kirki</i>	Kirk's dikdik
<i>Gazella gazella</i>	mountain gazelle
<i>Gazella dorcas</i>	dorcas gazelle
<i>Gazella thomsoni</i>	Thomson's gazelle = <i>Eudorcas thomsoni</i>
<i>Gazella subgutturosa</i>	goitered gazelle
<i>Gazella soemmerringi</i>	Soemmerring's gazelle = <i>Nanger soemmerringi</i>
<i>Gazella granti</i>	Grant's gazelle = <i>Nanger granti</i>
<i>Litocranius walleri</i>	gerenuk
<i>Antilope cervicapra</i>	Indian blackbuck
Oreotragini:	
<i>Oreotragus oreotragus</i>	klipspringer
Alcelaphini:	
<i>Connochaetes taurinus</i>	blue wildebeest
<i>Alcelaphus buselaphus</i>	hartebeest
<i>Damaliscus lunatus</i>	common tsessebe
<i>Damaliscus pygargus</i>	bontebok
Hippotragini:	
<i>Oryx gazella</i>	gemsbok
<i>Hippotragus niger</i>	sable antelope
<i>Hippotragus equinus</i>	roan antelope
Reduncini:	
<i>Kobus ellipsiprymnus</i>	waterbuck
<i>Kobus kob</i>	kob
<i>Kobus leche</i>	lechwe
<i>Kobus megaceros</i>	Nile lechwe
<i>Redunca arundinum</i>	southern reedbuck
Aepycerotini:	
<i>Aepyceros melampus</i>	impala
Caprini:	
<i>Ovis ammon</i>	argali
<i>Ovis canadensis</i>	bighorn sheep
<i>Ammotragus lervia</i>	Barbary sheep
<i>Capra ibex</i>	Alpine ibex
<i>Capra falconeri</i>	markhor
<i>Oreamnos americanus</i>	mountain goat
<i>Rupicapra rupicapra</i>	Alpine chamois

Table 2: Male and female behavioural characters (bibliographic source: Walther 1974).**Threat displays**

- 1) Pawing the ground (without urination or defecation) in hostile encounters.
- 2) Nose (vertically) upward posture in females.
- 3) Symbolic snapping in females.
- 4) Rising on hind legs in hostile encounters.
- 5) Dropping down onto knees.
- 6) Lateral head-shaking (like humans in negation).
- 7) Symbolic butting and/or head nodding (like humans in affirmation).
- 8) Downward sweep of head and horns.
- 9) Medial presentation of horns.
- 10) High presentation of horns.
- 11) Low presentation of horns.
- 12) Head low posture.

Dominance displays in hostile encounters**Broadside displays:**

- 13) Arched-neck posture.
- 14) Head-low posture.
- 15) Head-and-neck-stretched-forward posture.
- 16) Lifted-head posture.
- 17) Erected posture.

Frontal displays:

- 18) Head-turn (approximately 90°).
- 19) Erected posture.
- 20) Lifted-head posture.
- 21) Head-and-neck-stretched-forward posture.

Male courtship displays**Broadside displays:**

- 22) Head-low posture.
- 23) Head-and-neck-stretched-forward posture.
- 24) Lifted-head posture.
- 25) Erected posture.

Postures in following the female:

- 26) Head-turn (approximately at right angle).
- 27) Erected posture.
- 28) Lifted-head posture.
- 29) Head-and-neck-stretched-forward posture.
- 30) Arched-neck posture.
- 31) Head-low posture.

Laufschlag:

- 32) Kick with the foreleg combined with head-and-neck-stretched-forward posture.
- 33) Kick with the foreleg in normal or slightly erected posture.
- 34) Kick with the foreleg combined with lifted-head posture.

Mounting postures:

- 35) Mounting with chest, chin and sometimes also throat on the female's back.
- 36) Mounting with chest and nose (vertically) on the female's back.
- 37) Mounting with chest on the female's back, head and neck leaning forward but not touching the female's body.
- 38) Mounting with chest on the female's back, neck erected.
- 39) Mounting in standing or walking behind the female, chest not touching the female's back.

Table 3: Data matrix of behavioural characters in the studied taxa. Coding: 0 = character absent, 1 = character present, ? = undocumented.

	Threat												Dominance										Courtship																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	
Bos taurus	1	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	
Bos gaurus	1	0	0	0	0	1	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	
Bison bison	1	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	
Boselaphus tragocamelus	0	0	1	1	1	0	0	0	0	1	0	0	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Tragelaphus scriptus	0	1	1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	
Tragelaphus spekei	0	1	1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	
Tragelaphus angasi	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
Tragelaphus imberbis	0	1	1	0	0	1	1	0	1	0	1	1	0	0	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	
Tragelaphus strepsiceros	0	1	1	0	0	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	
Taurotragus oryx	0	1	1	0	0	1	0	1	1	0	1	1	1	0	0	1	1	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	
Cephalophus nigrifrons	1	0	1	0	0	0	0	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	
Raphiceros campestris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1
Madoqua kirkii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Oreotragus oreotragus	1	0	1	0	0	1	0	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Connocchaetes taurinus	1	0	0	0	1	1	1	0	1	0	1	1	1	1	0	0	1	1	?	?	?	?	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Alcelaphus buselaphus	1	0	0	0	1	0	1	0	1	0	1	1	0	1	0	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
Damaliscus lunatus	1	0	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	
Damaliscus pygargus	0	0	0	0	1	0	1	1	1	0	1	0	?	?	?	?	?	?	?	?	?	?	0	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	
Oryx gazella	1	0	0	0	1	0	1	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	
Hippotragus niger	1	0	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	
Hippotragus equinus	1	0	0	0	1	0	1	0	0	1	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	
Kobus ellipsiprymnus	0	1	1	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Kobus kob	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Kobus leche	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kobus megaceros	0	1	0	1	0	0	0	1	1	0	1	1	0	0	0	?	?	?	?	?	?	?	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
Redunca arundinum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Aepyceros melampus	0	0	1	1	0	1	1	1	1	0	1	1	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Gazella gazella	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	
Gazella dorcas	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	
Gazella thomsoni	1	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	
Gazella subgutturosa	1	0	0	0	0	0	1	1	1	1	1	1	0	?	?	?	?	?	?	?	?	?	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	
Gazella soemmerringui	1	0	0	0	0	1	0	0	1	0	1	1	?	?	?	?	?	?	?	?	?	?	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	
Gazella granti	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	
Litocranius walleri	1	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	
Antilope cervicapra	0	0	1	0	0	1	1	1	1	0	1	1	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	
Ovis ammon	1	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Ovis canadensis	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
Ammotragus lervia	0	0	0	1	0	0	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Capra ibex	0	0	0	1	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Capra falconeri	0	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Oreamnos americanus	1	0	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Rupicapra rupicapra	0	0	0	1	0	0	1	1	1	0	1	1	0	1	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	

sence of characters are coded 0 and 1 respectively, while undocumented characters are noted “?”. In order to simplify the phylogenetic resolution, we coded as present the characters that Walther (1974) considered as only possibly present. We considered that behaviour occasionally observed may constitute phylogenetically informative data. Of course this character coding should be reevaluated in further studies.

3.1.2 Behavioural phylogenetic analysis

The behavioural data matrix (Tab. 3) was analyzed by maximum parsimony under equal weights, using PAUP 4.0

4. Results

4.1 Taxonomic distribution of the behavioural characters

4.1.1 Threat displays

1) Pawing the ground: found in most bovid taxa: exceptions include Tragelaphini, Boselaphini, Aepycerotini, *Antilope cervicapra*, most of the Caprini (except *Ovis ammon* and *Oreamnos americanus*) and

Reduncini (except *Kobus leche*). This behaviour is also found in all other ruminant families. It may be a plesiomorphic feature linked to an ancestral pursuit deterrent signal expressed by a solitary, territorial species in response to the perception of a predator or a conspecific individual entering the territory.

As far as the Reduncini are concerned, it is interesting to note that none of the territorial waterbuck species mark their territory by establishing dung piles or with preorbital gland secretion (Walther 1974). This could indicate a less robust expression of territoriality in these species, similar to the Caprini, Tragelaphini and Boselaphini. The only surprising appearance for this character is in the Bovini, not typically considered territorial species, yet expressing this behaviour. This is in contrast to *Aepyceros melampus* and *Antilope cervicapra*, territorial species that do not express this behaviour.

oreotragus, *Kobus ellipsiprymnus* and *Cephalophus nigrifrons* may have acquired this character by convergence. This ancestral behaviour is also seen in other ruminant, nonruminant cetartiodactyls and even in perissodactyls. It may be a relict behaviour, retained in non-territorial species such as Tragelaphini and Boselaphini and in some territorial ones such as the four Antilopinae noted previously.

4) Rising on hind legs in hostile encounters: present in Caprini and seems to be synapomorphic for these taxa. Several other species express this behaviour (*Nanger granti*, *Aepyceros melampus*, *Boselaphus tragocamelus*, *Damaliscus lunatus*).

5) Dropping down onto knees: present in all Hippotragini and Alcelaphini species, and also by convergence in isolated species (*Bos taurus* and *Boselaphus tragocamelus* for Bovinae and *Kobus leche* for Antilopinae).

6) Head-shaking (like humans in negation): present in most of Bovinae (except *Bos taurus*, *Boselaphus* and *Taurotragus*) and in ten different Antilopinae species but without any tribal association which may indicate a high level of homoplasy.

7) Symbolic butting and/or head nodding (like humans in affirmation): present in most of Bovinae (except *Bos taurus* and *Boselaphus*), Hippotragini (except *Hippotragus niger*), Alcelaphini and several other Antilopinae species. Like the latter character, this feature seems to be homoplastic.

8) Downward sweep of head and horns: present in several species of different lineages. As with character 6 and 7, it seems to be highly homoplastic.

9) Medial presentation of horns: present in all bovid species except *Bos gaurus*, *Bison bison*, *Oryx gazella* and *Hippotragus equinus*. This character seems to be symplesiomorphic for bovid species.

10) High presentation of horns: present in all Hippotragini and *Gazella* species (except *G. soemmerringi*), and also by convergence in other species (*Tragelaphus goesi*, *Kobus ellipsiprymnus* and *Ovis ammon*).

11) Low presentation of horns: present in all bovid species except *Bison bison*, several Antilopinae species and a majority of the Caprini. This character seems to be plesiomorphic for bovid species.

12) Head low posture: present in all bovid species except *Bison bison*, several Antilopinae species and again a majority of Caprini. This character seems to be a bovid symplesiomorphy.

4.1.2 Dominance displays in hostile encounters

4.1.2.1 Broadside displays

13) Arched-neck posture: present in all bovid species except most of the Tragelaphini and Caprini, it seems to be a bovid symplesiomorphy.

14) Head-low posture: present in all Bovini and Alcelaphini species, and also likely by convergence in scattered species.

15) Head-and-neck-stretched-forward posture: present in *Tragelaphus* species and *Boselaphus* and by convergence in one *Gazella* and *Damaliscus* species. It appears to be highly homoplastic.

16) Lifted-head posture: present in most *Tragelaphus* species and *Boselaphus* and by convergence in several Antilopinae species.

17) Erected posture: present in all Antilopinae except most of Caprini, *Gazella dorcas* and *Eudorcas thomsoni*. Also present by convergence in *Tragelaphus angasi* and *Taurotragus oryx*. This character seems to be a synapomorphy of Antilopinae, lost in some species.

4.1.2.2 Frontal displays

18) Head-turn (approximately 90°): present in all bovid species with some notable exceptions: *Bos gaurus*, most *Tragelaphus* species, *Boselaphus*, and several species within Antilopinae. This character seems to be symplesiomorphic for bovids.

19) Erected posture: present in all bovid species except most species of *Tragelaphus*, *Boselaphus*, several species within the Caprini and most species of *Gazella*. This character seems to be symplesiomorphic for bovids, its loss being synapomorphic for the clades mentioned.

20) Lifted-head posture: present in several tribes including the Antilopini, Caprini, and Reduncini. It is also found in several species of *Tragelaphus* and Antilopinae, perhaps through convergence. It appears to be highly homoplastic.

21) Head-and-neck-stretched-forward posture: present in most species of *Tragelaphus* and *Boselaphus*. It is also found in several species of Antilopinae, perhaps through convergence.

4.1.3 Male courtship displays

4.1.3.1 Broadside displays

22) Head-low posture: present only in three species of Bovinae: *Bison bison*, *Tragelaphus angasi* and *T. strepsiceros*, possibly convergent.

23) Head-and-neck-stretched-forward posture: present in all Tragelaphini, Boselaphini and Bovini (except *Bos taurus*). It seems to be synapomorphic for these taxa. Several other clades have acquired this character, perhaps by convergence (in *Gazella*, Alcelaphini, and twice in Caprini).

24) Lifted-head posture: present in all Bovini and also by convergence in different tribes.

25) Erected posture: present in several bovid species. It seems highly homoplastic.

4.1.3.2 Postures in following the female

26) Head-turn (approximately at right angle): present in most of Tragelaphini and Boselaphini and in several bovid species. It seems highly homoplastic.

27) Erected posture: present in all bovids except in Bovini and Alcelaphini. This character seems to be a bovid symplesiomorphy, lost in the two mentioned clades.

28) Lifted-head posture: present in *Nanger*, all *Gazella* and all Bovini species. It appears in several other disparate species, perhaps through convergence.

29) Head-and-neck-stretched-forward posture: present in all bovids with the following exceptions: Hippotragini and two species from the Bovini. This character seems to be a bovid symplesiomorphy, lost in the two mentioned clades.

30) Arched-neck posture: present only in three Antilopinae species: *Gazella gazella* and two species of *Damaliscus*.

31) Head-low posture: present only in two *Tragelaphus* species, and *Kobus megaceros*.

4.1.3.3 Laufschiag

32) Kick with the foreleg combined with head-and-neck-stretched-forward posture: present in all Caprini (except *Ammotragus*) and two *Gazella*.

33) Kick with the foreleg in normal or slightly erected posture: absent in all Bovinae, present in most of Antilopinae tribes except Alcelaphini. It seems to constitute a synapomorphy of Antilopinae.

34) Kick with the foreleg combined with lifted-head posture: present only in *Nanger granti*, *Eudorcas thomsoni*, *Antilope* and *Litocranius*.

4.1.3.4 Mounting postures

35) Mounting with chest, chin and sometimes also throat on the female's back: present in all species of Bovinae. This behaviour seems to be an unambiguous synapomorphy for this clade if compared to the mounting postures in outgroups: male Cervidae mount with the chest and nose vertically on the female's back (Dubost 1971), whereas Antilocapridae (O'Gara 1990), Moschidae (Green 1985) and Giraffidae (Cap 2006) are characterized by mounting with chest on the female's back, head more or less erected.

36) Mounting with chest and nose (vertically) on the female's back: present in all Alcelaphini species (synapomorphy) and possibly by convergence in *Cephalophus*, *Oreamnos* and *Boselaphus tragocamelus*. These species share this trait with all cervids (plesiomorphic or convergent).

37) Mounting with chest on the female's back, head and neck leaning forward but not touching the female's body: present in two *Kobus* species, and possibly by convergence in *Rupicapra* and *Cephalophus*.

38) Mounting with chest on the female's back, neck erected: absent in Bovinae (synapomorphy) and present in most of Antilopinae except Alcelaphini, two *Gazella* species, *Cephalophus*, and *Antilope*.

This behaviour, also expressed by pronghorns, giraffids and moschids, seems plesiomorphic for Bovidae.

39) Mounting in standing or walking behind the female, chest not touching the female's back: present in all Antilopini, *Madoqua*, *Litocranius* and *Raphicerus* (hence some Antilopini also present posture 38 with chest on female's back).

4.2 Behavioural phylogenetic patterns

The phylogenetic tree generated from the maximum parsimony analysis of all behavioural characters with equal weights is presented in Fig. 2. Only one alternative equiparsimonious topology was found. The consensus of these two trees is largely unresolved, and there is no Bremer support or significant bootstrap support for the clades (very low CI and RI, only 52 % bootstrap support for Tragelaphini). Hence, in its present state, our tentative behaviour-based phylogeny should not be considered as challenging current molecular or morphological phylogenetic analyses. In Fig. 2, the clade (*Oreotragus*, *Kobus ellipsiprymnus*, *Ovis*, *Capra*) joins with *Ammotragus lervia*, *Redunca arundinum*, *Oreamnos americanus* and two species of *Kobus*. In the alternative tree, the clade (*Oreotragus*, *Kobus ellipsiprymnus*, *Ovis*, *Capra*) is positioned as sister group of the clade including both *Kobus leche* and *Tragelaphus*, the remainder of the topology being otherwise unchanged. We comment only on the first topology because it shows a more plausible arrangement of Caprini relative to previous morphological and molecular analyses (e.g. Vrba & Schaller 2000; Hassanin et al. 2012).

Node 1

- Bovidae: the ancestral bovid ethotype appears to have exhibited the following behaviour: pawing the ground (character **1**); presentation of horns high and low (**9** and **11**) and head low posture (**12**) in threat displays; arched-neck posture (**13**) in dominance broadside displays; head-turn (**18**) and erected posture (**19**) in dominance frontal displays; head-and-neck-stretched-forward posture (**29**) during male courtship displays in following the female; and mounting with chest, chin and sometimes also throat on the female's back (**35**). The latter behaviour could also be an apomorphy of Bovinae, shared by Bovini, Tragelaphini and Boselaphini (this group is not monophyletic in this tree).

- Bovini: Several characters are shared by species within the Bovini (*Bos taurus*, *B. gaurus* and *Bison bison*): Head-low posture (**14**) during broadside dominance displays which is also present by convergence in Alcelaphini and several disparate Antilopinae species. Lifted-head posture in broadside displays (**24**) and in following the female (**28**) during male courtship are behaviours also present in this

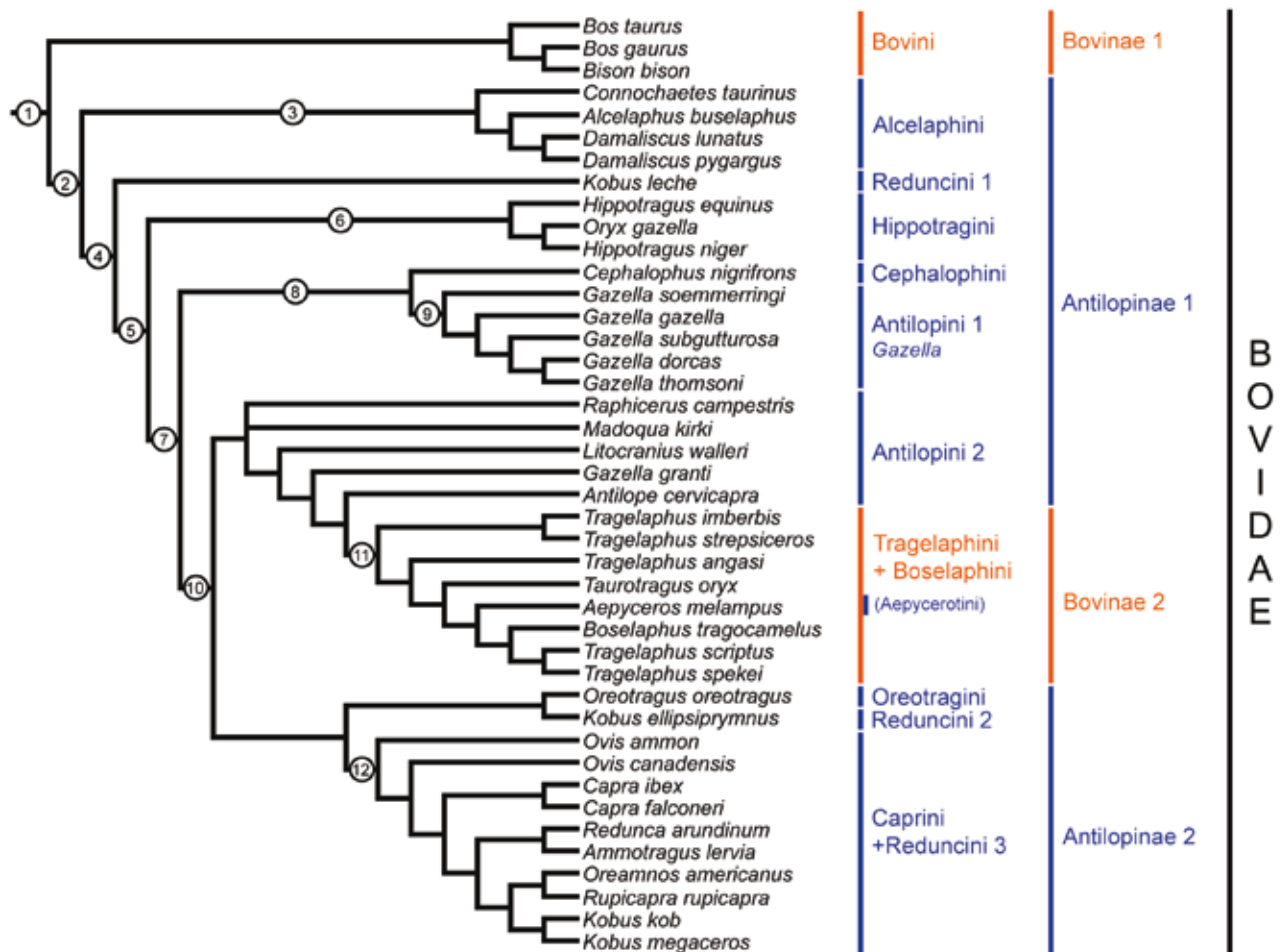


Figure 2: Most parsimonious tree supported by behavioural data from Walther (1974). Tree length = 215 steps; CI = 0.18; RI = 0.54. Each node labeled with a number refers to descriptions of synapomorphies in the text.

group. These are also found in other tribes.

Node 2

Antilopinae + (Tragelaphini, Boselaphini): This group is characterized by erected posture in dominance broadside displays (17), a character found in a majority of the Antilopinae studied. It is also present in *Tragelaphus angasi* and *Taurotragus oryx* perhaps through convergence. The latter species also share the same reversions of lifted-head posture in broadside displays (24) and in following the female (28), but they do not mount with chest, chin and sometimes throat on the female's back (35).

Node 3

Alcelaphini: head-low posture (14) during broadside dominance displays appears to be an informative character. This character is also present in all Bovini and in a few other isolated species possibly due to convergence. Head-and-neck-stretched-forward posture (23) during male courtship broadside displays is similar in its distribution. The only unambiguous synapomorphy in this group is mounting with chest and nose (vertically) on the female's back

(36), present also in *Cephalophus*, *Oreamnos* and *Boselaphus*.

Node 4

This group contains Tragelaphini, Boselaphini, and all Antilopinae tribes except Alcelaphini. It is characterized by kick with the foreleg in normal or slightly erected posture (33), except for Tragelaphini and Boselaphini; this character is not found in any Bovinae. Likewise, this group displays mounting with chest on the female's back, neck erected (38), again absent in the Bovinae (Bovini, Tragelaphini, Boselaphini). This grouping at node 4 is in conflict with most molecular-based phylogenies (Hassanin et al. 2012), according to which it would appear as polyphyletic, linking parts of the Antilopinae to parts of the Bovinae. These 'unifying' behavioural characters may simply be synapomorphies of most Antilopinae; Tragelaphini and Boselaphini being misplaced due to convergence in several highly homoplastic characters (see nodes 10 and 11 below).

Node 5

The same group as the previous one without *Ko-*

bus leche: males in this group display erect posture when following a female during courtship (27). As noted above, members of the Tragelaphini, Boselaphini and Antilopinae could have arrived at this behaviour through convergence.

Node 6

Hippotragini: This tribe presents its horns high (10) as opposed to the medial presentation of horns (9) in other groups. Members of this tribe do not display the head-turn in frontal dominance displays (18) nor head-and-neck-stretched-forward posture (29) during male courtship displays in following the female. These two losses may be adaptations to the large size of the horns in these species (Lundrigan 1996).

Node 7

This group contains Tragelaphini, Boselaphini, and all Antilopinae tribes except Alcelaphini and Hippotragini, and *Kobus leche*. The only informative character is the loss of dropping down onto knees (5), present in Hippotragini and Alcelaphini and in isolated species from other groups (*Bos taurus* and *Boselaphus tragocamelus* for Bovinae and *Kobus leche* for Antilopinae). This character seems to be synapomorphic for each clade if the true topology follows other behavioural, morphological (Vrba & Schaller 2000) and molecular analyses (Hassanin et al. 2012).

Node 8

Cephalophini + Antilopini 1 (*Gazella*): These tribes show two losses: erect posture in dominance frontal displays (19) and mounting with chest on the female's back, neck erected (38).

Node 9

Gazella: This genus (notably without *Nanger granti*) appears monophyletic, and shows three informative characters: head-and-neck-stretched-forward posture in male broadside courtship displays (23), lifted-head posture in following the female (28), and mounting in standing or walking behind the female, chest not touching the female's back (39). Characters 23 and 28 seem to be convergent with Tragelaphini, Boselaphini and Bovini. Character 39 is interesting because it is also present in other Antilopini species: *Antilope*, *Madoqua*, *Litocranius* and *Raphicerus*, so it could be a synapomorphy for the entire tribe.

Node 10

This group contains Tragelaphini, Boselaphini + Antilopini 2 + Oreotragini + Reduncini + Caprini and is characterized by three characters (6, 16, 20) generally presenting a high level of homoplasy, and con-

tributing to the misplacement of Tragelaphini and Boselaphini among Antilopinae.

Node 11

Tragelaphini + Boselaphini: these Bovinae tribes show two informative characters; the first explains, in part, their apparently false position (separated from Bovini) because head-and-neck-stretched-forward posture in male courtship broadside displays (23) is also present by convergence in *Gazella* species and Alcelaphini, and two species of Caprini. The second character (35) corresponds to a likely Bovinae synapomorphy with mounting with chest, chin and in some instances also throat on the female's back.

Node 12

Caprini (united with parts of Reduncini in the tree, see Fig. 2): this tribe appears monophyletic with two synapomorphies. Rising on hindlegs in hostile encounters (4) is also expressed by several other species (*Nanger granti*, *Aepyceros melampus*, *Boselaphus tragocamelus*, *Damaliscus lunatus*). An evolutionary explanation could be a functional link between the morphology of horns and the techniques of ritualized sparring displays in all Caprini species (Lundrigan 1996). The loss of low presentation of horns (11) is convergent with *Bison bison*, and several Antilopinae species.

5. Conclusions

This tentative behavioural phylogenetic analysis of bovids should be considered with caution. It is a preliminary work, relying on data obtained by reviewing the literature. Little phylogenetic resolution could have been expected given the reduced data set of 39 characters for 42 taxa, and the high rate of undocumented characters in some species. Despite these limitations, some of the tribes and larger clades defined by morphological or molecular analyses are supported in this behavioural analysis. But numerous points of discrepancy do exist between this behaviour-based phylogeny and morphology- or molecular-based phylogenies. Among the unusual placements, the scattering of the genus *Kobus* is partly explainable by the high rate of undocumented characters in these species. The splitting of Bovinae is due to some highly homoplastic and plesiomorphic characters, but it must be noted that character 35 "mounting with chest, chin and sometimes also throat on the female's back" is exclusively shared by Bovini, Tragelaphini and Boselaphini. Given the diversity of mounting postures, this character could be considered as a particularly reliable one, constituting a non-ambiguous synapomorphy of Bovinae if mapped on both the molecular and morphological phylogenies of Fig. 1. The genus

Gazella is supported in our analysis, while *Nanger granti* is placed outside this clade, which is consensual in itself, but its far distant position in our phylogeny represents a major departure from the morphological and molecular-based analyses. Here again the mounting posture “standing behind the female” (39) would tend to cluster *Nanger granti* closer to *Gazella*. This character is also present in *Litocranius walleri* and *Antilope cervicapra*. So, concerning the unusual splitting of Bovinae and Antilopini in our analysis, and mixing of parts of these groups, it seems that giving more weight to mounting postures could partly correct such rather obvious misplacements.

Another important character in bovids seems to be the laufschiag pattern and especially 33 “kick with the foreleg in normal or slightly erected posture” (Walther 1974): absent in all Bovinae, present in most of Antilopinae tribes except Alcelaphini, it could be a synapomorphy of Antilopinae, and would effectively appear as such if mapped on the phylogenies of Fig. 1.

Of course, given the lasting difficulty for devising sophisticated evolutionary models for some kinds of behavioural characters, the best way to improve behavioural phylogenetics of ruminants remains to control for the accuracy of the available data, obtain data missing for some species, and expand the range of studied characters and species. Sources of relevant behavioural phylogenetic characters are diverse, as testified by the phylogenetic analysis of vocal behaviour in Cervidae (Cap et al. 2008). The major limitation of such investigations remains the enormity of the task of reliably documenting behavioural repertoires from multiple observations in the field or under comparable experimental conditions and the scarcity of such studies. A coordinated effort for documenting and cross-validating a common behavioural data base could be an efficient solution requiring motivation and a cooperative spirit.

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